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CONTRIBUTIONS TO THE EMBRYOLOGY OF THE AMERICAN EEL (*ANGUILLA ROSTRATA* LESUEUR)

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(Figs. 103–116 incl.)*

OUTLINE

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[1] Contribution, New York Zoological Society Department of Tropical Research, No. 250.
* Figs. 103–109, 114 and 116 drawn by Dr. Charles J. Fish; Figs. 110–113 after Eigenmann; Fig. 115 after Schmidt.

I. THE ARCTURUS SPECIMENS

Collection and Description of Eggs

The one-hundredth station made by the "Arcturus Oceanographical Expedition," on July 15, 16, and 17, 1925, proved to be an extremely interesting collecting-ground, not only because certain specimens were taken here which were found nowhere else, but

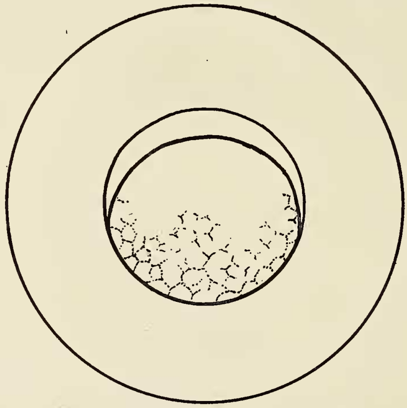

Fig. 103. Egg of American eel, July 16, 1925, probably very soon after fertilization.

because the immediate locality had been worked upon in former years by the "Challenger," "Plankton," and "Bache Expeditions," and later by the Danish Commission for the Exploration of the Sea under the direction of Johannes Schmidt. This position (lat. 32° 02′ N. long. 65° 00′ W. at noon on July 16) is approximately ten miles southwest of Bermuda on the Challenger Bank, a shoal about five miles in diameter and only twenty-four fathoms at its shallowest depth. Intensive collecting carried on in the deeper regions on the edge of the Bank revealed a rich marine life.

On July 16 four eggs were found in a Petersen young fish trawl from five hundred fathoms, the lowest of a line of nets towed at various levels. These tiny specimens closely resembled the few known eggs of eels and eel-like fishes. They were highly transparent, colorless except for a slight yellowish tinge of the yolk, and measured 3.3 millimeters in outside diameter (Fig. 103). No oil globules were present. They were further characterized by a very wide perivitelline space, the diameter of the yolk measuring 1.7 millimeters. A very early stage in development had been reached, the germinal

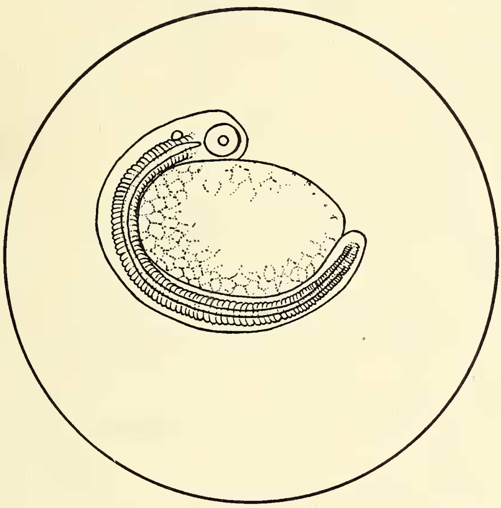

Fig. 104. Egg of American eel about 88 hours after stage shown in Fig. 103.

disc defined but without evidence of cleavage. The eggs did not float at the surface but remained near the bottom of the fingerbowl until hatched. Because of the small number of eggs and the difficulty of microscopic work on shipboard, the notes were unfortunately rather fragmentary.

Embryology and Larval Development

At 9 A.M. on July 17 the cleavage stages were past and the embryo barely defined, reaching about one-quarter around the yolk.

Three days later (9 A.M., July 20) the embryo had reached two-thirds around the yolk, and yolk and embryo maintained a position uppermost in the egg. The embryo was elongated, colorless; muscle segments, eyes, auditory vesicles, notachord, and yolk blastopore well differentiated. The yolk was vesicular, as is the case in certain clupeiods, appearing under the microscope as though it were broken up into a mass of cells.

On the eighth day (8.30 A.M., July 23) the embryo in one egg was nearly around the yolk, and very active—the whole embryo pulsating rapidly. The vertebrae and pectoral fins were prominent. Black pigmentation had begun in the rim and iris of the eye, and the pupil was gray. The embryo in another egg was further advanced, had lost the very elongated shape and become more flattened laterally and proportionately much deeper. There was more black pigment in the iris than in the preceding stage. A third egg had the black pigment confined to a tiny bar on the upper margin of the eye with two dots below. The heart was very active. The pronounced beak-like projection of the upper jaw, and the vesicular yolk with a narrow stalk extending backward nearly to the region of the vent were typical of a muraenoid embryo. This embryo was more than two-thirds around the egg, situated high up.

The fourth egg hatched between midnight and 8 A.M. on July 23, approximately one week after fertilization. During this incubation period the temperature of the water in which the eggs were kept had varied from 27.7° centigrade when cleavage began, to 23.9° centigrade at hatching. From the egg emerged a leptocephalus 9 millimeters long, very transparent, and colorless except for ocular pigment. In life there appeared to be a very few black chromatophores on the caudal portion of the embryonic fin, but as this region was somewhat mutilated after death, their presence cannot definitely be established. The larva was very slow in its movements the first day, floating motionless near the surface and swimming only when disturbed.

Fig. 105 shows the leptocephalus when first observed. There is no suggestion of an oil globule and the yolk is completely absorbed. The embryonic fin envelops the body without trace of finray formation. The hypural elements are not evident. The pectorals are prominent and the teeth well developed, as Fig. 106 shows, three pairs resembling fangs in the upper jaw, and four pairs in the lower.

On July 24 the three remaining eggs were dead, but the larva seemed to be thriving well. It swam rapidly and almost constantly with characteristic eel-like motion. The length at twenty-four hours was 10 millimeters. Fig. 107, made one day after Fig. 4, shows the rapid development of the teeth.

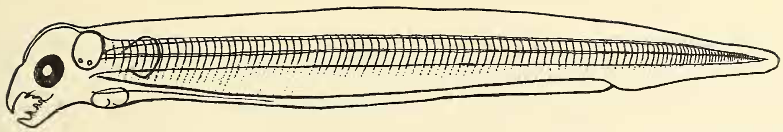

Fig. 105. Prelarva of American eel soon after hatching, 9 mm. long. (8 A.M., July 23)

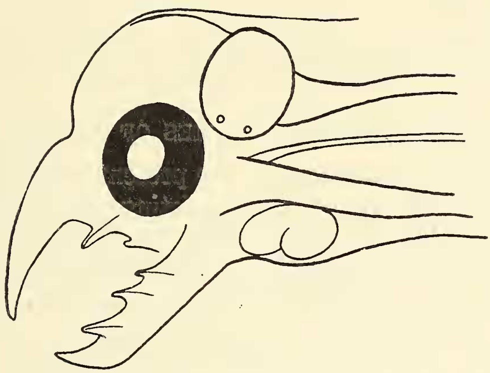

Fig. 106. Head of prelarva shown in Fig. 105.

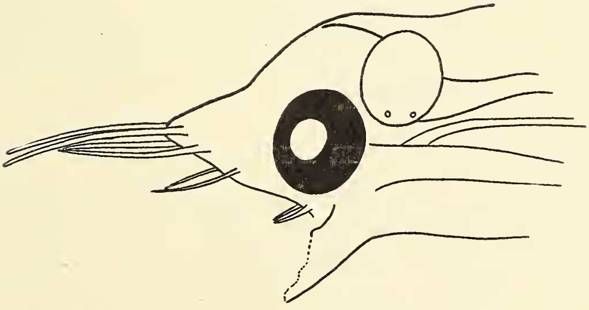

Fig. 107. Head of same prelarva shown in Fig. 106 one day later, demonstrating the extremely rapid development of prelarval teeth.

On the morning of July 25 the larva had died and was considerably shriveled. It had been impossible before, because of the activity of the single larva, to count the segments, and the determination in the injured condition was difficult. There were, however, between 105 and 110 muscle segments, this small difference in recorded number made necessary by the almost indistinguishable caudal myomeres. An embryo freed from the egg was found to have at least 105 and not more than 109 segments, about 64 of them preanal and 41 postanal.

II. COMPARISON WITH PREVIOUSLY DESCRIBED MURAENOID EGGS

Five Unidentified Species of Raffaele

Before attempting to identify the present specimens, it will be necessary to examine carefully the existing knowledge concerning young eels. In 1888 at the Naples Zoological Laboratory, F. Raffaele hatched out the pelagic eggs of five species of eels, collected from August to November, and found certain characters common to them all:

1) very large size distinguishing them at first glance from the other eggs taken,
2) large perivitelline space,
3) delicate egg membrane without pore canals, ordinarily with iridescent reflections,
4) structure of yolk, being entirely vesicular.

The differences between the various species, as shown on the chart p. 295, were in size, in the presence and number of oil globules, in pigmentation, and especially in the number of muscle segments in the embryos which developed.

Unfertilized Conger Eggs (*Leptocephalus conger*)

In 1891 J. T. Cunningham described the unfertilized eggs of a conger eel, which he obtained at the Southport Aquarium, England, on July 24, 1889. The eggs were squeezed from the female and one measured, after the formation of the perivitelline space, 1.6 millimeters. The formation of the perivitelline, which occurred within an hour after extrusion, indicated to Cunningham that the eggs were nearly ripe but not that they had necessarily acquired the char-

Raffaele's Species	Character of the Egg			Character of the Larva
	Diameter	Oil Globules	Description	
No. 6	2.0–2.5 mm.	1 (for the most part)—5, of 0.3–0.35 mm.	Perivitelline space very broad; yolk vesicular, diameter 1.2–1.3 mm. On third day of incubation swelling occurs on oesophagus (oesophageal pouch).	Abdominal segments 72 (73?). Larva very elongate, compressed. Head relatively small; intestine not open posteriorly but ending about halfway to the edge of the ventral finfold; fourth ventricle of heart enormous; on second or third day of life outside the egg the mouth opens and it develops long and pointed teeth in the two jaws; at same time there appear 6 large black pigment spots along trunk ventrally.
No. 7	More than 3.0 mm.	6–12, which, during development of embryo, occupy posterior part of yolk.	(Note: Schmidt, 1913, believes quite certainly that this is *O. hispanus*, same as Boeke's No. 3.)	Abdominal segments 59 (60?). Differs from preceding principally in its shorter length, and the absence of pigment spots.
No. 8	2.0–2.5 mm.	More than 30, usually yellowish, scattered over the whole distal surface of yolk.	Similar to No. 6 but perivitelline space a little narrower.	Abdominal segments 72 (73?).
No. 9	2.0 mm.	1, club-shaped and placed anteriorly during development of embryo.	Vitellus attached to membrane by filaments.	Abdominal segments 66 (67?). Similar to No. 6 but very much narrower.
No. 10	2.7 mm.	None		Abdominal segments 44 (45?). Similar to No. 6.

The present species may be compared with those of Raffaele:

Present species	3.3 mm.	None	Perivitelline space broader than others, diameter 1.7 mm.; yolk vesicular.	Abdominal segments 64; elongate, compressed, intestine ending at margin of ventral finfold; fourth ventricle enlarged; mouth open and teeth well developed at hatching; no ventral line of pigment spots but few near extremity of caudal finfold, and eye pigmented in embryo.

acteristics that would show in the perfectly ripe egg. They were chalk-white, opaque, with no oil globules, and sank to the bottom in seawater of density 1.027.

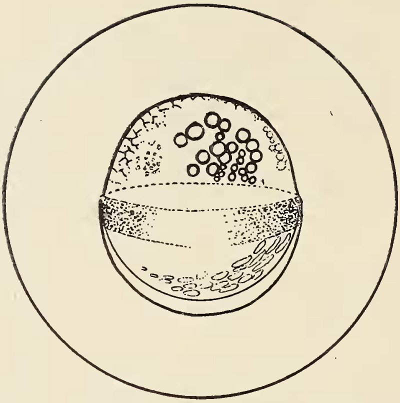

Fig. 108. Egg of Species No. 7 of Raffaele. Drawn from Raffaele.

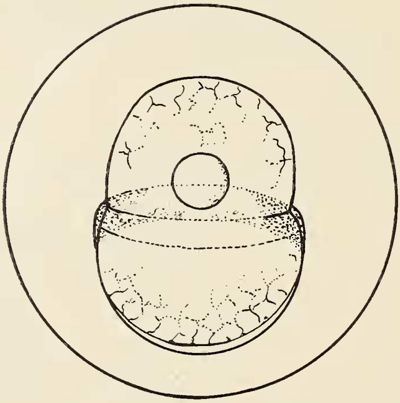

Fig. 109. Egg of Species No. 6 of Raffaele. Drawn from Raffaele.

An Unidentified Egg Believed by Some Investigators to be The European Eel (*Anguilla vulgaris*)

Five years after the unfertilized conger egg had been reported, 1896, Grassi and Calandruccio identified as the common European eel one of the eggs of Raffaele's list. "From the study of Raffaele on pelagic eggs, I have come to the conclusion that the eggs of his undetermined species No. 10, having a diameter of 2.7 millimeters and differing from all the others in the absence of oil globules, must belong to the *Anguilla vulgaris,* because from them Dr. Raffaele obtained prae-larvae which had only forty-four abdominal myomeres." Concerning their seasonal distribution, Grassi states: "Eggs which according to every probability belong to the common eel, are found in the sea from the month of August to that of January inclusive."

This identification has been questioned by E. W. L. Holt (1907) on the ground that it is at variance with our knowledge of the unripe ovarian eggs of the European eel, but he gives no description of the egg as he believes it to be. The prelarva 6 millimeters long figured by Schmidt (1924) has a large oil globule which would seem to evidence the same occurrence in the egg. On the other hand Syrski's (1873) observations support the belief in an absence of oil globules in an immature condition. "The ovaries of young eels of the length of about 500 millimeters contained invariably little fat and the eggs were without globules." The larger of these ovarian eggs measured about 0.2 to 0.25 millimeters in diameter.

The same difference of opinion prevails concerning the immature egg of the American species. Bigelow (1924) states: "Eel eggs have not been seen, but certainly they are provided with an oil globule, as this is present in unripe ovarian eggs and in the vestiges of the yolk sac of the youngest embryos." However Eigenmann (1901), in discussing eel eggs which might occur in American waters, takes the opposite stand: "The common eel egg has been identified as one without an oil globule." He is doubtless confusing the American and European species, basing his statement on Grassi and Calandruccio's disputed claim to the identification of the European eel egg.

Some "silver eels," or eels which have begun their seaward migration and are clothed in spawning attire, I placed alive in a salt water aquarium at the U. S. Bureau of Fisheries at Woods Hole, Mass., in November, 1925. On February 5, 1926, one specimen, 70 centimeters long, was found in a dying condition. The ovaries were examined and found to contain unripe eggs of various sizes up to 0.25 millimeters. Another eel, 66 centimeters long, which died on April 8, contained eggs up to 0.32 millimeters. A third specimen, on May 5, had eggs up to 0.32 millimeters, also.

The last silver eel was examined on December 22, 1926. During thirteen months of confinement this specimen had not eaten, although it had been tempted with squid and other foods, nor had it changed, apparently, in size. The ova within measured up to 0.45 millimeters, the largest, to my knowledge, which have been recorded. The experiment is being repeated this year, and it is hoped that these eels may be kept alive for even longer periods.

Fertilized Egg, Embryology, and Larval Development of the Conger

The first American contribution to the embryology of muraenoids was made in 1901 when Carl H. Eigenmann succeeded in hatching out some eggs which he provisionally identified as those of the conger eel (*Leptocephalus conger*). Eigenmann's drawings and careful descriptions have been of great value in comparison with the present species. The eggs were taken by the U. S. B. F. Schooner *Grampus* on the tile-fish grounds, about thirty miles south of South Shoal, off Nantucket, Mass., on July 31, 1900. Hitherto eel eggs had been found only in the Mediterranean, and even there they had been observed within a limited area.

(1) Description Of Egg.—The eggs described by Eigenmann were very similar to Raffaele's No. 6.

Species	*Diameter of Egg*	*Character of of Vitellus*	*Oil Globules*	*Abdominal Segments*
No. 6 (Raffaele)	2.0–2.5 mm.	1.2–1.5 mm. diameter	1–3 of 0.3–0.35 mm.	72 (73?)
Conger eel (Eigenmann)	2.4–2.75 mm. (Six pre-served eggs measuring 3 mm. may be identified with these)	1.75–2.0 mm. diameter	1–6 light yellows of variable size	65–71

The conger eggs, as shown above, measured 2.4 to 2.75 millimeters from membrane to membrane; the vitellus measured 1.75 to

2.0 millimeters and was of the vesicular texture typical of all eel eggs. There were from one to six oil globules of variable size. When several were present, one was always much larger than the others.

(2) Development Of Yolk.—The yolk of the conger eggs had certain characteristics in common with the present egg. Its bulk was in the usual position with a narrow stalk extending backward below the intestine nearly to the region of the vent. The anterior portion was broadly rounded when first observed by Eigenmann (Fig. 110). As development went on, however, and the yolk diminished

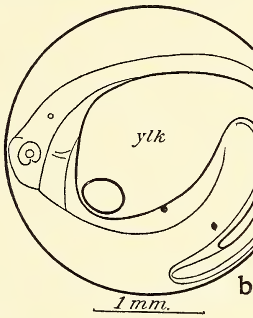

Fig. 110. Egg of conger eel when first observed, showing characteristic shape of yolk.

in size, the most anterior part became more and more constricted until it formed a mere protuberance enclosing the oil sphere. In the present embryos, which contained no oil spheres, the anterior contour apparently remained rounded. By further constriction the oil sphere of the conger egg became elongate, and the posterior stalk of the yolk beneath the alimentary canal somewhat larger as its anterior part diminished. In succeeding stages the slender yolk sac acted as a pericardial chamber. The yolk sac was observed disappearing at wide intervals along its entire length by constrictions which deepened gradually until a series of minute globules more or less widely separated from each other were all that remained.

Some of the eggs were found hatching on August 3, the third day after the stage observed in Fig. 110. The jaws of many of these were gaping, a condition not found in those which took several days longer to hatch. Eigenmann believed the gaping jaws to be an abnormality which might be due to an unusually early hatching.

(3) Jaws.—The development of the jaws is a character which differs considerably in the conger and the eel described in the present

paper. Fig. 111 shows a conger larva soon after hatching. The mouth is not distinguishable. Fig. 112 shows a larva two days later with the jaws in a stage of development which was passed in the present eel several days before hatching. Fig. 113 is the conger larva about three days after hatching. The mouth is in about the same condition as the present one when first observed, (see Fig. 105), less than twelve hours after hatching, or hardly more developed than that of the embryo several days before.

Raffaele first observed the mouth opening on the second day after hatching. This was followed by a rapid development of the teeth. There were three pairs in the upper jaw, a character in common with the present leptocephalus. Eigenmann's conger developed four pairs in the upper jaw, graded from front to back, the anterior ones comparatively enormous fangs. In the lower jaw of his specimens were four pairs of more uniform size, the second one larger than the others. A condition of which he questions the normality is the appearance of five pairs of teeth in the lower jaw of the oldest individual. The present species had four pairs in the lower jaw.

(4) Color.—In the conger color appeared first in the tail region, and the following six spots were evident above the alimentary canal and along the margin of the myotomes of the tail on the second day of larval life: (1) about middle of yolk, (2) halfway between this and end of yolk, (3) at end of yolk, (4) in front of anus, (5) some distance behind anus, (6) about the tip of tail. These spots were placed in approximately the same location as the enlargements formed by the constriction of the yolk sac. More pigment spots appeared between those already formed, but the number was constant in larvae of the same age, although the relative and actual size varied greatly in individuals. A few pigment cells appeared in the upper jaw, and a few scattered cells near the tip of the lower jaw developed later into a well-marked spot.

The presence of pigment in the conger differs decidedly from that of the present eel. Although the latter was not kept alive until the time when chromatophores would have appeared in the conger, the eye had pigment in the embryo before hatching. It had appeared first as a tiny bar on the upper margin of the eyeball with two dots below. A slightly later stage had the whole outer margin of black with large blotches over the iris, and the pupil gray. At hatching the iris was solid black. The formation of pigment in the

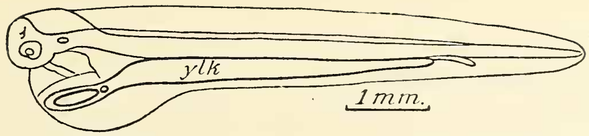

Fig. 111. Prelarva of conger eel soon after hatching.

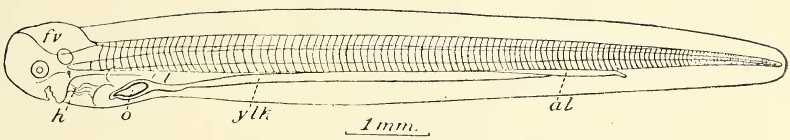

Fig. 112. Prelarva of conger eel two days later than stage shown in Fig. 111.

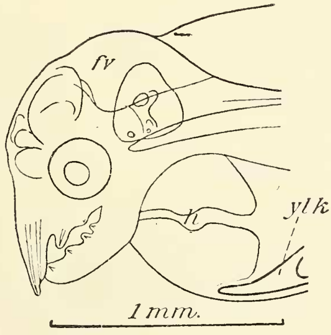

Fig. 113. Head of conger eel prelarva about 3½ days old.

eye of the conger occurred with its first appearance on the body, about three days after hatching.

(5) Finfold.—The finfold of the conger is continuous from the nape to the yolk sac. In the species described in this paper, how-

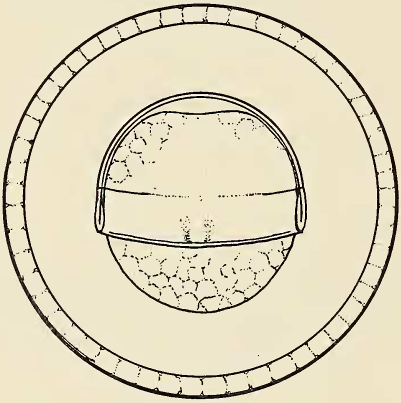

Fig. 114. Egg of Muraena No. 7 of Boeke, showing the type of muraenoid egg which has a delicate inner membrane attached by filaments to the outer capsule. Drawn from Boeke.

ever, the finfold apparently extends from the nape only to the anus, which is located back three-fourths of the distance between tip of jaws and end of tail. If the finfold does continue forward below the intestine, it is so narrow that it was indistinguishable in the living specimen. The intestine of the conger, although equal in length at this stage, lies just below the muscle segments, and even in the latest stages observed by Eigenmann (about eleven days after hatching) the intestine was remote from the margin of the ventral finfold, which continued forward to the remaining fragments of the yolk.

Nine Unidentified Species of Boeke.

In 1903 J. Boeke described the eggs of nine species of eels, taken during the summer months of 1900 and 1901 near the Zoological Station at Naples. Five of these species had previously been recorded by Raffaele (1888). The characteristics of the various eggs are indicated below.

Species	Character of the Egg			Character of the Larva
	Diameter	Oil Globules	Description	
Muraena No. 1 (No. 6 Raf.)	1.8–2 mm.	1–5 lying close together.	Perivitelline space very broad; diameter yolk 1.1–1.3 mm. Mouth and anus closed in egg.	Abdominal segments 67–72. When yolk completely absorbed, length about 10–15 mm., sharp teeth, and 6 pigment spots on trunk.
Muraena No. 2.	3.3 mm.	7–12, somewhat smaller than those of Mur. No. 1 and not so thickly grouped.	Diameter yolk 1.7 mm. Mouth and anus open in egg.	Abdominal segments 75–77. Teeth and 6 pigment spots formed before hatching. Length at hatching about 7–8 mm.; at absorption yolk about 15 mm.
Muraena No. 3 (No. 7 Raf.)	3.3 mm.	As Mur. No. 2.	As Mur. No. 2.	As Mur. No. 2 but with abdominal segments 59 (60?).
Muraena No. 4 (No. 8 Raf.)	2.2 mm.	30 or more.	Diameter yolk 1.4 mm. Mouth and anus closed at hatching.	Abdominal segments 65–67 at absorption of yolk.
Muraena No. 5	2.9 mm.	Many, small globules concentrated into opaque, whitish mass about size of a single globule in Mur. No. 1.	Diameter yolk 1.5 mm. Mouth open and teeth formed in egg.	Abdominal segments 58–60.
Muraena No. 6 (No. 9 Raf.)	Somewhat smaller than Mur. No. 1.	1, long drawn-out shape like tear.	Double membrane to egg capsule, inner delicate and attached by filaments to outer.	Abdominal segments at hatching 59. Abdominal segments at absorption of yolk 63. (Raf. gives 66 (67?)).
Muraena No. 7.	2.6 mm.	None.	Diameter yolk 1.5 mm. Capsule as in Mur. No. 6.	Abdominal segments 54 (55). Colorless except for few pigment cells at anus and tail end.
Muraena No. 8 (No. 10 Raf.)	2.6 mm.	None.	As Mur. No. 7.	As Mur. No. 7 but with abdominal segments 44 (45?).
Muraena No. 9	2 mm.	10–16 quite closely congregated.	Diameter yolk 1.1 mm. Double capsule as in Mur. No. 6.	Prelarva died a short time after hatching and no segment count obtained.

Muraena conger.

Schmidt (1913) described the eggs of another conger, *Muraena helena,* which were widely distributed in the upper layers of the Mediterranean over and near the coastal banks during July, August, and September. The eggs measured 4–4.5 millimeters and were without oil globules. They were further characterized by a thick capsule, large perivitelline space, and the embryos had from 144 to 148 muscle segments.

Nettastoma melanurum.

Large numbers of the eggs of *Nettastoma melanurum* Raf. were taken by Schmidt in the Baleatic and Tyrrhenian Seas. They occurred in the surface as well as in the deeper layers during January and February, being the only muraenoid eggs collected on the winter Mediterranean cruises of the *Thor*. They measured 2 to 3 millimeters in diameter and contained no oil globules. The embryos were without teeth or pigment and had from 55 to 60 preanal myomeres. Older leptocephali (12–82 millimeters) referred to this species had 63–66 preanal and c. 140–143 postanal myomeres.

Ophichthys hispanus and Ophichthys serpens.

Schmidt has identified Raffaele's "Species No. 7" and Boeke's "Muraena No. 3" with *Ophichthys hispanus*, and the latter's "Muraena No. 2" with *Ophichthys serpens*. In both species the mouth is open and most of the characteristic preanal pigment, "gut patches," are developed before the embryo is hatched. The yolk sac is stalked, as in other muraenoids, and the "borsa stomacale" or local swellings of the digestive tract are very large.

III. COMPARISON WITH PREVIOUSLY DESCRIBED LEPTOCEPHALI AND ADULT EELS

Distribution

Were the number of Atlantic fishes that pass through a leptocephalic stage small, our task of determining the present specimen would be lightened. The records of previous expeditions, however, show many such larvae, at least forty-five species having been completely (with vertebral count) described, as well as fifteen or more species of adults of which the leptocephalid young have not yet been distinguished. That some of these species remain in the larval form for long periods, as the three-year leptocephalus of the European eel (*Anguilla vulgaris*), and the fact that during this stage the animal is carried about passively by currents, leads us to expect certain ones in far separated localities. For this reason, again, we are unable to narrow our list of possibilities to a very few.

Almost nothing is known concerning the places of spawning of muraenoids, so that it is not possible to interpret our eggs on the

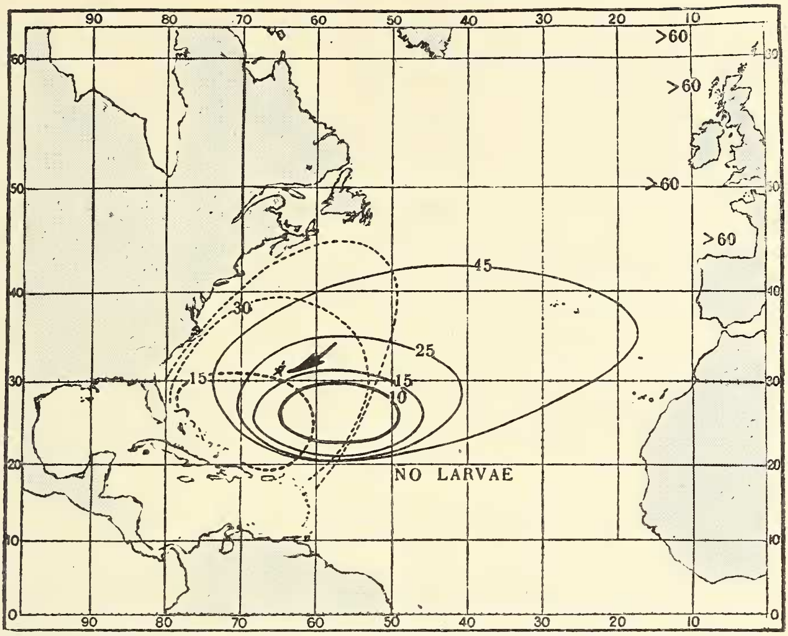

Fig. 115. European Eel (*Anguilla vulgaris*) and American Eel (*Anguilla rostrata*)

Breeding areas and distribution of larvae shown by curves; dotted for American, continuous for the European species. The heavily-drawn innermost curves embrace the breeding areas of the two species. The curves show limits of occurrence; i. e. specimens less than 25 mm. in length have only been found inside the 25 mm. curve, etc. The cross (x) marks the spot where the present American eel eggs were taken.

basis of such knowledge alone. We do know, however, that the station from which they came was very close to, if not well within, the limits of the breeding grounds of both the American eel, *Anguilla rostrata,* and the European eel, *Anguilla vulgaris.* The cross (x) on Fig. 115 marks the location of these eggs, lat. 32° 02′ N., long. 65° 00′ W. It is just outside the curve which designates the breeding area of the American eel and within which all larvae were smaller than 15 millimeters, and is within the 25 millimeter length curve of the European eel. Schmidt (1924) notes the limits of larval *Anguilla* distribution as follows:

American eel (*Anguilla rostrata*) larvae

Northernmost find:	Lat. 42° 19′ N., long. 50° 22′ W.
Southernmost find:	Lat. 17° 55′ N., long. 64° 48′ W.
Westernmost find:	Long. 82° 59′ W., lat. 20° 08′ N.
Easternmost find:	Long. 50° 22′ W., lat. 42° 19′ N.

European eel (Anguilla vulgaris) larvae

Northernmost find: Lat. 61° 21′ N., long. 10° 59′ W.
Southernmost find: Lat. 20° 14′ N., long. 57° 03′ W.
Westernmost find: Long. 73° 43′ W., lat. 35° 42′ N.
Easternmost find: Long. 15° 35′ W., lat. 38° 07′ N.

Prelarva Of European Eel.

The illustration by Schmidt of an European eel six millimeters long shows decided differences from the present prelarva, although the general proportions of the body and the teeth are strikingly

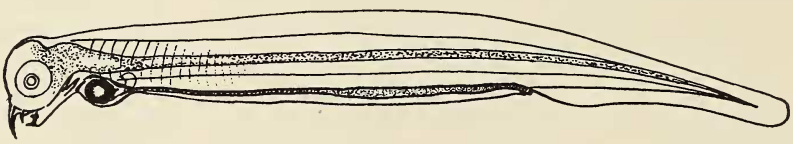

Fig. 116. Smallest known prelarva of European eel, 6 mm. in length. Drawn from Schmidt.

similar. The eye of the European eel is pigmentless, whereas the eye of this eel is black; a large oil globule serves to differentiate it further. The presence of pigment on the caudal portion of the embryonic fin is probably identical in the two species (see p. 292).

Prelarva Of American Eel

The smallest American eel prelarva previously recorded was pictured by Schmidt (1916). It measured 10½ millimeters after preservation and was obviously in a later stage of development than my specimen. The dental formula $\frac{1+3}{1+3}$ was identical in the two prelarvae, but the teeth of Schmidt's specimen were more even, stronger and less tapering, like those of older leptocephali. The depth of the body of the latter was slightly greater, a change which is known to occur as development progresses. Pigmentation, as in the present specimen, was restricted to the eye and a few black stellate chromatophores on the embryonic fin near the tip of the tail (not on the tail itself). The number of myomeres was the same.

Myomere Count

A character which remains constant throughout the life history of the eel—through the prelarval, leptocephalid, hemilarval, elver, and adult stages—is the number of muscle segments or vertebrae. This has been the principle accepted for distinguishing species. Einar Lea (1910) examined the records and descriptions of all species of young and adult eels and found those which give the vertebral count limited to twelve species with larval stages known, twenty-three species with larval stages unknown, and forty-four unidentified larvae. Weber (1913) added descriptions of seven more species taken by the Siboga Expedition, but none of these were Atlantic forms. The chart following is taken from Lea's work on the *Michael sars* muraenoid larvae (1910), with the addition of species subsequently recorded, and includes all those eels for which I have found the myomere count.

Name of Species	Number of Segments	Name of Species	Number of Segments
SPECIES, THE LARVAL STAGES OF		larva:	199–206
WHICH ARE KNOWN		*Ophichthys serpens* (Linnaeus)	208
Cyema atrum Gunther	73	larva:	209–212
larva: *L. cyematis atri*	75–77	*Saurenchelys cancrivora* Ptrs.	200
Anguilla rostrata LeSueur	103–113	larva: *L. oxyrynchus*	240–249
larva: *L. grassi*	105–109	SPECIES, THE LARVAL STAGES OF	
Anguilla mauritiana Bennett		WHICH ARE NOT YET IDENTIFIED	
larva:	105–108	*Muraenesox coniceps* Jord. & Gil-	
Gastrostomus bairdii Gill & Ryder	110	Gilbert	111
larva: *L. gastrostomi bairdii*	108	*Anguilla japonica* (Schleg.)	112–119
Anguilla vulgaris Turt.	111–119	*Echidua catenata* Bleek	116
larva: *L. brevirostris*	111–119	*Gymnothorax meleagris* Shaw	120
Congromuraena balearica de la		*Gymnothorax nebulosus* Bl.	122
Roche	about 130	*Echidua cocosa* Garm.	...
larva: *L. taenia, inornatus, diaph-*		*Echidua nebulosa* Garm.	...
onus, eckmani	123–137	*Echidua scabra* Garm.	123
Chlopsis bicolor Raf.	133	*Moringua raitaborua* Ham.	126
larva:	131–136	*Gymnothorax undulatus* Lacep.	126
Congromuraena mystax de la Roche	about 138	*Histiobranchus infernalis* Gill	130
larva: *L. haeckeli, yarrelli, bibro-*		*Ilyophis brunneus* Gilb.	127–132
ni, gegenbauri, kollikeri,		*Ophichthys ocellatus* Les.	132
stenops (in part)	132–147	*Echidua zebra* Bleek	132
Muraena helena Lin.	139–143	*Gymnothorax unicolor* de la Roche	134–135
larva:	140–143	*Ophichthys gomesi* Casteln.	136–140
Synaphobranchi pinnatus Gronov	146–151	*Gymnothorax ocellatus* Agas.	....
larva: *L. synaphobranchi pinnati*	144–157	*Gymnothorax moringa* Cuv.	141
Conger vulgaris Cuv.	146–164	*Conger marginatus* Val.	142
larva: *L. stenops* (in part), *mor-*		*Serrivomer sector* Garm.	144
risii, punctatus	142–159	*Muraenesox cinereus* Forsk.	145
Ophichthys hispanus (Bellotti)	154–159	*Ophichthys frontalis* Garm.	149
larva:	154–159	*Xenomystax rictus* Garm.	154
Ophichthys imberbis (de la Roche)	156–159	*Gordiichthys irretitus* Jord. & Davis	157
larva:	156–159	Garman	173
Nettastoma melanurum Raffaele		Jord. & Davis	225

Name of Species	Number of Segments	Name of Species	Number of Segments
LARVAL FORMS, NOT IDENTIFIED		*Leptocephalus longidens* Garm.	140
Leptocephalus taenia Lesson	106–115	" *strommani* E. and K.	141
" *similis* Lea	110	" *thorianus* Schmidt	142
" *holti* Schm.	112	" *morrisii* E. and K.	142
" *peterseni* Weber	112	" *oculus* Peters	c.142
" *indicus* Weber	115	" *hjorti* Weber	144
" *diptychus* E. and K.	122	" *mucronatus* E. and K.	144–147
" *euryurus* Lea	116–117	" *megacara* Lea	149–150
" *obtusus* Garm.	119	" *falcidens* Garm.	about 153
" *dentex* Cantor	about 120	" *ingolfianus* Schm.	153–155
" *rex* E. and K.	119–123	" *discus* E. and K.	155–159
" *dentatus* Garm.	121	" *lanceolatus* Stromm	158–163
" *amphioxus* E. and K	122	" *enchodon* Lea	158
" *spinocadux* Lea	125	" *humilis* E. and K.	157–162
" *michael-sarsi* Lea	127	" *lanceolatoides*	
" *anguilloides* Schmidt	132	Schmidt	163
" *caudomaculatus* E.		" *lychnus* Garm.	165
and K.	133	" *gilberti* E. and K.	180
" *mysticus* Lea	about 127	" *hjorti* Blegvad	182
" *cingulus* Garm.	131–133	" *rostratus* Schmidt	188–191
" *dolichorhynchus* Lea	128–136	" *urosema* Lea	190
" *latus* E. and K.	133	" *telescopicus* Schmidt	200–210
" *histiobranchi infer-*		" *canaricus* Lea	200–220
nalis or *Ilyophidis*		" *stylurus* Lea	218–229
brunnei Lea	133–134	" *latissimus* Schmidt	240
" *splendens* Lea	135	" *andreae* Schmidt	about 250
" *acus* Garm.	135	" *sicarius* Garm.	" 250
" *schmidti* Weber	135	" *mirabilis* Brauer	293
" *gilli* E. and K.	137	" *polymerus* Lea	about 443
" *cinctus* Garm.	138		

Such differences as the number of finrays, which have been used alone by certain describers to differentiate species, are often useful to supplement the myomere count, for we find individuals of the same species varying somewhat as well as more than one species with the same number of muscle segments.

IV. IDENTIFICATION AS AMERICAN EEL

By comparing our specimen with the above list we see that the known leptocephalus of *Anguilla rostrata*, the American eel, which has been described as *Leptocephalus grassii* Eigenmann and Kennedy, is nearest, the number of muscle segments coinciding exactly. No other species of which the larval stage is known comes within twenty of this count except the European eel, *A. mauritiana*, and *Gastrostomus bairdii*. The hatched specimen as well as the embryos removed from the eggs have less than 111 segments, and the other differences in pigmentation and the absence of an oil globule, make it reasonably safe for us to eliminate the European species. *A. mauritiana* is barred by its distribution, being a member of the Indo-Pacific fauna but not of the Atlantic.

The leptocephalus of *Gastrostomus bairdii* has a like count, but although no young of this species has been taken smaller than 33 millimeters, Einar Lea believes that the smaller stages would be of the type of leptocephali described as *Leptocephalus latus* by Schmidt (1909), and later as *Leptocephalus latissimus*. It has a deep, leaf-shaped body, totally unlike the form of the present leptocephalus.

Muraenesox coniceps, an adult form described by Jordan and Davis (1888) has 111 segments but is found only in the Pacific Ocean. A closely related Atlantic species, *M. savanna*, ranges from Cuba to Rio Janiero, but the myomere count is not recorded. The young of the two species have not been seen, and the slightly greater number of segments is our only negative evidence.

The distribution of *Anguilla japonica*, which is found only in the northwestern Pacific, would preclude this species, as would the larger segment count.

Leptocephalus similis Einar Lea has 110 segments, but the short high head and rounded tail are quite unlike this specimen. The same differences are evident between it and *Leptocephalus euryurus* Einar Lea, a species taken near the coast of Morocco, having 116 segments.

Weber gives the number of segments of two specimens of *Leptocephalus taenia* Lesson taken by the Siboga Expedition as 106 and 115. This species, however, has the intestine terminating almost at the posterior end of the body, different dentition, and other characteristics distinguishing it definitely from ours.

A specimen of *Leptocephalus peterseni* Weber has 112 muscle segments, but here again the form of the body is entirely different, being deeper and less tapering posteriorly, and the shape of the head and the teeth are peculiar.

Leptocephalus indicus Weber, taken in the Sulu-See, has 115 myomeres, but the species would hardly have so wide a distribution. Only one specimen, 115 millimeters long, is known.

By the above process of elimination it seems evident that of those species for which the number of muscle segments is known, only the American eel can qualify for consideration. Had we descriptions of the young of all living eels, we might with certainty attribute our leptocephalus to this particular species. Every expedition at sea, however, captures more new species, and so it is only provisionally that we call these eggs and the young developing from them *Anguilla rostrata.* The evidence for this identification may be summed up as follows:

1. Character Of The Eggs

The eggs were definitely those of an eel or eel-like fish, evidenced by their large size, large perivitelline space, vesicular-stalked yolk, and slightly iridescent cell-membrane, which was fine in texture and showed no pore canals, as well as by the leptocephalid character of the larvae hatching from them. They were different from any muraenoid eggs previously observed.

2. Location Of The Collecting Ground

The eggs were found within the same general area designated by Schmidt to encompass the breeding grounds of the American and European eels, and without doubt had been floating only a very short time. The latter fact is indicated by the early stage of development reached at the time of capture (germinal disc defined but without evidence of cleavage) and the rapidity with which incubation proceeded. The first egg hatched in seven days. It is impossible to say exactly how far above the bottom they were floating, but the trawl was towed at 500 fathoms below the surface in water of between 500 and 2116 fathoms depth.

The depths at which eels spawn and their eggs develop have been speculated upon by various investigators, but no actual data have been secured. Raffaele believed spawning to take place at great depths and the eggs to remain there unless some unusual condition caused a few to mount higher in the sea. Eigenmann attacked the latter conclusion on the ground that Grassi had found eggs of eels at the surface, and all species were typical of pelagic eggs, being lighter than water, having oil spheres and other characteristics of eggs which normally live in the surface layers. He remarks: " 'If fertilization takes place at great depths' it must be 'only exceptionally, for unknown reasons,' that they remain at the great depths. The fact that Raffaele never secured eggs younger than when the gastrula was well formed would favor the supposition that they were fertilized at a great depth and rose slowly in the water."

In the absence of closing net hauls it is impossible to state at just what level our eggs were taken. At the time of their collection four surface nets were towing, meter nets at 300 and 400 fathoms, and a meter net and a Petersen young fish trawl at 500 fathoms. The fact that no eggs were taken in the meter net at the same depth would seem to mean that the eggs were not abundant, or that they drifted by higher up after the other nets had been hauled. The Petersen trawl was at the end of the cable and in its hauling towed through the levels where the other nets had been. The meshes of the various plankton nets on the line were sufficiently small to retain eggs of this size had they entered, but were it not for a red shrimp and a few transparent sagittae which helped to imprison them, the eggs would no doubt have passed through the half-inch meshes of the trawl. The shrimp is typical of the Intermediate or Black Zone, so-called, about 800 to 1500 meters, and the Sagittae of the Transition Zone which is, in this region, about 400 to 800 meters.

If we were able to conclude, from the fact that the eggs were collected only by the deepest net, that they were taken while towing at 500 fathoms and not during its passage from this depth to the surface, then the early stage of development attained would favor the theory of fertilization at great depths.

3. Comparison Of This Prelarva With The Smallest Known European Eel

Since the two species *Anguilla rostrata* and *Anguilla vulgaris* are so closely allied that distinction is based mostly upon a difference of only a few muscle segments, it is logical to suppose that the earliest larval stages will show like similarity. The present prelarva strikingly resembles the European eel prelarva in the general proportions of the body and the teeth, but the pigmented eye and the absence of an oil globule, as well as the difference in myomere count, show them to be separate species.

4. Comparison Of This Prelarva With The Smallest Known American Eel

Schmidt (1916) figures a prelarva of this species 10½ millimeters long, which, although in a later stage of development, has many characters in common with my specimen. The dental formula $\frac{1+3}{1+3}$ is identical in the two prelarvae, but the teeth of Schmidt's specimen were more even, stronger, and less tapering, like those of older leptocephali. The depth of the body of the latter was slightly greater, a change which is known to occur as development progresses. Pigmentation in both prelarvae was restricted to the eye and a few black chromatophores on the embryonic fin near the tip of the tail. The number of myotomes (104–110 in Schmidt's eel, 105–109 in this) was the same.

5. Myomere Count

A character which remains constant throughout all stages of development is the number of muscle segments and vertebrae. According to the principle adopted by most investigators interested in the eel question, "A species is regarded as new when it differs from all species formerly described where the number of muscle-segments is stated" (Lea). This leptocephalus has the same number of muscle segments as the American eel, and no other larva known from Atlantic waters nor adult species of an eel (except G. bairdii) has this count. Of those species which have a number of muscles segments within twenty of the present specimen, there are other specific differences which allow their elimination (i.e. *Anguilla vulgaris, Anguilla mauritiana, Anguilla japonica, Gastrostomus bairdii, Muraenesox coniceps, Leptocephalus similis, Leptocephalus taenia, Leptocephalus peterseni,* and *Leptocephalus indicus*).

Our specimens, with approximately 105 to 109 segments, may be compared with seven young eels identified as *Leptocephalus grassii*, taken at Woods Hole, Mass., during the summer of 1900, in which the count was 106, 107, 107, 108, 109, 110, and 107, as recorded by Eigenmann and Kennedy (1901), and with the count of ten elvers 50 to 60 millimeters in length taken at random from many collected on May 20, 1926, in the U. S. Fisheries Boat Basin, Woods Hole—104, 106, 106, 106, 107, 105, 107, 111, 108, and 108.

V. HISTORY OF THE EEL QUESTION

Theories Concerning the Reproductive Methods of the Eel and the Sexual Organs

The difficulty in determining our scant number of eggs, four in all with only one living long enough to hatch, can be better understood when we consider the enigma which the eel question has always presented. It was not until 1874 that a male specimen was distinguished and a controversy which had lasted for almost twenty-three centuries ended. Many great scientists of all times have speculated upon the mysterious reproductive methods of the eel. In 1880 Jacoby published an interesting history of man's attempt to solve this question, which beliefs we may profitably review here, for the floundering of these writers concerning eel reproduction, in strong contrast to their other attainments, in many cases, surely demonstrates the difficulty of the problem. When the early Greeks failed to find spawn and milt within the eel, they jokingly named Jupiter as the father of these fishes, to whom they were in the habit of ascribing all children of doubtful parentage.

The first record of a serious attempt at explanation was made by Aristotle (384–322 B.C.), some three hundred and fifty years before Christ. This great master of thought contended that eels as well as smaller animals were born from the earthworms *Lumbricus terrestris,* which, in turn, were produced spontaneously from mud and moist soil. Aristotle came to this conclusion even though he had previously recognized, "by the crackling of the eggs when placed over fire," the ovaries of the "grongo" (*Leptocephalus conger*).

In the first century after Christ the Roman scholar Pliny the Elder, (Gaius Plinius Secundus, 23–79 A.D., author of "Naturalis historia," a work in its present form consisting of thirty-seven books), ventured the belief that young eels were produced from fragments rubbed off by the adults against the rocks, a different version of the abiogenetic myth.

Athenaeus and Oppian held the same opinion, varying it sometimes to the procreation from a slimy mass produced by the rubbing together of their bodies.

Albertus Magnus, writing in 1254, repeated again the hypothesis that the rubbing of eels against the rocks produced young, but added that, he had been told, eels could also be born alive.

Three hundred years later, 1555, Rondelet brought forward two entirely different ideas. He maintained that young were produced from putrified matter as well as by eggs resulting from the copulation of male and female eels. In 1558 the writings of Konrad von Gesner (1516–1565) echo these two methods of reproduction.

The next suggestion, and one which was held by many succeeding scientists, was that of Marcello Malpighi (1628–1694), great student of physiology and anatomy. An expert microscopist, also, Malpighi was the first to apply the microscope to the study of plant and animal structure. Such discoveries are attributed to Malpighi as the first actual observation of capillary circulation, the structure of secreting glands, and of the lower stratum of the epidermis, the vasicular coils of the cortex of the kidneys, the follicular bodies in the spleen, and the first knowledge of the finer anatomy of the brain,—and yet this keen observer failed to identify correctly the ovaries of eels and eel-like fishes, as the "grongo" (*Leptocephalus conger*) and the "muraena" (*Muraena helena*), believing these organs to be deposits of fat and giving them the name of "striae adiposae."

Other microscopists failed to recognize as such the eel ovaries. Francisco Redi in 1684 identified unmistakably those of the "muraena" but not those of the eel. A noteworthy achievement of this scientist, however, was the refutation of the theory that eels are born from decaying matter. The "young eels" which others had found within the adults, and on which evidence partly was based the belief in viviparity, Redi showed were intestinal worms and firmly contended that eels reproduced by the spawning of eggs. Redi and Cristian Franz Paullini, living also in the seventeenth century, were the first to bring forward the belief that the reproduction was not unlike that of other fishes, although they did not themselves observe the eggs and semen within the eels.

A contemporary of Redi was the famous Dutch microscopist Anthony von Leeuwenhoek (1632–1723), whose researches gave us our first description of blood corpuscles, detailed accounts of the structure of muscle tissue, the crystalline lens, and the teeth. In examining the urinary bladder of an eel, Leeuwenhoek found a number of minute parasitic worms. The bladder, he maintained, was the uterus and the worms within were young eels. A common belief at this time was that eels were produced from dew.

Georg Elsner reported having seen an eel with uterus full of young.

In 1710 Professor Antonio Vallisneri of the University of Padua pictured the real ovaries, but following the theories of those before him, believed them to be fatty organs, "vasi adiposi." In one specimen he found a swim-bladder deformed by disease, and not recognizing it as a pathological condition, announced that he had at last discovered the "true ovary" of the eel. The small round granules which he mistook for eggs were later shown by Mundini to be swelled glands.

Vallisneri's assertion caused grave doubts and heated discussions among the Academy of Bologna scientists, and so possessed with a desire to discover the ovaries were they that, Jacoby relates, Professor Pietro Molinelli promised several fishermen of Comacchio a large reward for a pregnant eel. In 1752 a live eel was brought to him with stomach much distended, and found to be full of eggs. The crafty fisherman, with an eye to the reward no doubt, had opened up the specimen and crammed the stomach with the eggs of another fish.

Carl von Linné (1707–1778), known to biology as the founder of the binary system of nomenclature and author of more than one hundred and eighty published works, adhered to the doctrine that eels were viviparous.

It was not until 1777 that the ovary of the eel was recognized, the honor of the discovery belonging to Carlo Mundini, professor of anatomy at the University of Bologna. An eel resembling that described by Vallisneri seventy years before was caught near Comacchio, sent to the Academy of Bologna, and subsequently given to Professor Cajetan Monti. Too ill at the time to examine the specimen himself, Professor Monti, in consulatation with some of his scientific associates, resolved to turn the investigation over to Mundini. The latter's description and excellent drawings, however, although given on May 19, 1777, to the Academy of Bologna, were not published until 1783. Three years previous, in 1780, Otto Friedrich Müller published the finding of eggs within the eel, but certain inaccuracies in his statement tend to give Mundini precedence.

The notable achievement of Mundini was not to stand undisputed and a few years after it was attacked by Lazzaro Spallanzani (1729–1799), who professed to have examined four hundred and ninety-seven eels without being able to confirm the former's discovery. He maintained that the ovaries shown by Mundini were merely unusually fat folds of the diaphragm. It has been pointed out, however, that Spallanzani's attack smacks more of personal animosity than of just criticism based on conflicting results.

Martin Heinrich Rathke, writing between 1824 and 1850, again gave a detailed account of the eel ovary, quite accurately describing the egg within. He added little, however, to the work of Mundini. His article, published in "Müller's Archiv" in 1850 on a pregnant eel examined by him, permanently settled the dispute.

Certain mistakes in Rathke's work were corrected in 1874 by Syrski, Director of the Museum of Natural Sciences at Trieste and professor in the University of Lemburg. This scientist has the honor of first recognizing the spermatic organs of the eel. The search for the male, which, thus, did not end until ninety-six years after the finding of the ovaries, was also marked by erroneous beliefs.

In 1872 Reinhold Hornbaum-Hornschuch had stated the discovery of a male individual, indicated by the possession of round bodies enclosing small granules, in the fringed bodies of a number of eels, where eggs appear in the female.

So difficult of solution was the question that leading zoologists of the day were forced to conclude that "eels may reproduce by means of parthenogenesis, or by being of different sex, or also by being hermaphrodites."

Two years before the work of Syrski, Professor Giovanni Battisto Ercolani at Liepzig asserted in memoir-form, with illustrations, that he had found both the true testicle and a rudimentary testicle within the eel. Syrski, however, showed the "true testicle" to be a sac on the left side formed exceptionally by the peritoneum, and corresponding in position to a mass of fat attached to the swim-bladder between the right ovary and the intestine, which mass Ercolani termed the "rudimentary testicle." The "self-moving spermatozoa" found on the walls of this sac were shown to be fat, the movements of which were due merely to the molecular movements of granules found often in animal tissue. The "alveolar or proligenous cells of the testicle" were the common alveolar vessels of adipose tissue.

Other investigators, G. Balsano Crivelli and L. Maggi, believed that they had found the testicles in these fatty deposits, which, Syrski tells us, are found in nearly all of his specimens, "more developed on the right side than on the left, sometimes fringed, as shown in the illustration accompanying Ercolani's article, or with long borders, as shown in Prof. Maggi's illustration, but always of a structure which is, so to speak, typical of adipose tissue."

In 1874 R. Eberhard of Rostock described an "embryo of an eel" 24 millimeters long, with very large head and eye, swollen belly, and a yellow yolk sac. This specimen had supposedly come from the abdominal cavity of an eel and was one of about a thousand similar embryos contained therein.

In the same year Professor Münter, director of the Zoological Museum of Greifswald, after examining about three thousand eels without finding a male specimen, concluded that eels must necessarily reproduce by parthenogenesis. The eggs were laid in all probability at the bottom of the Baltic Sea from the middle of March to the middle of April, according to this investigator, and without fertilization developed into young eels one-half to two inches long, which migrated into fresh water about the beginning of May.

Causes of Erroneous Beliefs

There are several logical reasons why this problem eluded solution for some two thousand two hundred and twenty-four years, since, for the first time of which we have record, it was considered by Aristotle. The general structure of the organs contributed much to the difficulty. The ovarian organs resemble those of a few fishes, the salmons and sturgeons for example, but are unlike those of the majority. They are two ribbons of tissue covered by tiny leaflets arranged transversally, on the outer surface, running almost the whole length of the body cavity to right and left of the intestinal canal. The spermatic organs are made up of two rows of very tiny lobes, about fifty on each side, connected by vasa deferentia running almost the whole length of the body cavity. In young eels of 200–300 millimeters or less the testicles have not yet attained the lobulated form and are similar to the ovaries of the female. The greatest length of the male specimens examined by Syrski was 430 millimeters, showing the males to be smaller than the females. The fact that the testicles are easy of differentiation only in specimens between 400 and 430 millimeters is one reason why they were not identified for so long a period.

That the American eel nearing a spawning condition seeks the open sea and does not feed for some time previous explains why specimens with completely ripe eggs have not been taken.

Some beliefs and superstitions concerning the procreation of the eel are not as far-fetched as they would seem at first glance, and we can explain their origin among unscientific observers. In Germany, Norway, and Sweden the eel-like fish *Zoarces viviparus* is called the Aal-mutter, or eel-mother. The young of Zoarces, as its name implies, are born alive and have constantly been confused with young eels. Thus we explain the "eel embryo" of Eberhard.

The idea of attributing the parentage of eels to other fishes has been carried beyond reasonable comprehension. Jacoby tells us that in Comacchio the fishermen believe even the changes in color and shape of the common mullet, *Mugil cephalus*, cause the differences in color and shape of eels, that eels copulate with water snakes, and—impossible as it may seem!—the Sardinian fishermen claim a beetle, *Dysticus roeselii*, as the "eel-mother." It has been pointed out that the confusion may have occurred from the finding of the aquatic hair-worm Gordius in this beetle, and because Dysticus and the eel often live in the same waters, the laughable relationship has been claimed.

A superstition concerning Gordius is that each individual is born from a horsehair dropped into water where a horse has been drinking. This means of reproduction has been stretched to include the eel, doubtless confused with the worm-body of Gordius.

No wonder centuries and centuries of questioning and speculation passed before science could dispel such superstitions—and indeed in some parts of the world today it has not succeeded.

Location Of The Spawning Ground

With the truth finally established that the eel, just as other fishes, possesses ovaries and testes, the next obstacle to investigators seeking a solution of the eel question was the location of the breeding ground. Various writers had expressed the belief that spawning and fertilization took place offshore at depths varying from ten feet to the abysses of the ocean. Others maintained that they hatched in fresh water, as Robert B. Roosevelt, in 1877, who claimed his trout ponds in Great South Bay, Long Island, harbored breeding eels. To some the explanation of young eels coming upstream and overland on damp nights has not been sufficient to account for their presence far from the coast, often in landlocked water, and there are many today who scoff at an open sea migration theory.

Such stories as the following are prevalent among intelligent people, and it is a difficult task to convince them otherwise. In 1886 the Bulletin of the U. S. Fish Commission contained this statement by J. N. Sawyer, a Delaware eel-fisherman, "While some of them do (go to salt water to spawn), I do not think they all do, for in the winter of 1836 or 1837 we had what is known as the January flood in the Delaware, and wagonloads of eels of all sizes were found on low places after the water had subsided. One of my neighbors built a very tight dam, so constructed as not to permit any fish or eels to ascend. By this he overflowed a tract of land, and placing some eels in the pond left them to breed. After a period of fifteen or twenty years he placed an eel-weir in the dam and drew off the water to drain the pond for a meadow, catching barrels of eels of all sizes. These instances cited proved to me that eels do not all return to salt water to spawn, but spawn wherever they find suitable places in ponds or streams."

In spite of the popular tendency to discredit an exclusively-ocean spawning place, however, it was long ago noticed that in the fall of the year adult eels migrate downstream, and in the spring great numbers of tiny eels, about six to seven centimeters in length, appear from somewhere, swarming upon the coast and swimming upstream into fresh water, back over the course their parents took outward to the sea. Smaller young were never seen and it was not until 1896 that their dissimilarity to the adult was guessed. In that year Grassi and Calandruccio published the amazing discovery that the peculiar ribbon-like fish described by Kaup in 1856 as *Leptocephalus brevirostris* was indeed the larva of the European eel, and further answered the question of their absence inshore by declaring that the eel must spawn at great depths, the leptocephali normally developing and living at this level. Their presence at the surface in the Straits of Messina was explained by the action of currents churning up the bottom layers of water. The probability of development very far below the surface has not been confirmed, and many workers at the present time are doubtful of its occurrence in any eels, all evidence strongly pointing against larval life at such depths for the American and European eels at least.

The greatest advances toward an understanding of the breeding places of the eel have been made by the Danish Commission for the Exploration of the Sea under the directorship of Johs. Schmidt.

From 1904 until the present Schmidt has been working in masterly fashion and the conclusions of his latest report sums up briefly his achievements in the life history of the European eel. "During the autumn months the silvery eels leave the lakes and rivers and move out into the sea. Once beyond fresh-water limits the eels are, in most parts of Europe, outside our range of observation. Exceptions are, however, found, as in the case of the Danish sounds and belts and adjacent waters, which are passed by great quantities of eels on their way to the Atlantic, and form the site of important fisheries about October. In the western part of the English Channel trawlers may, toward the end of the year, occasionally bring up a few big specimens in their nets, but after this the last trace of the eel on European ground is lost. No longer subject to pursuit by man, hosts of eels from the most distant corners of our continent can now shape their course southwest across the ocean, as their ancestors for unnumbered generations have done before them. How long the journey lasts we can not say, but we know now the destination sought: A certain area situate in the western Atlantic, southeast and north of the West Indies. Here lie the breeding grounds of the eel.

"Spawning commences in early spring, lasting to well on in summer. The tiny larvae, 7–15 mm. long, float in water layers about 200–300 meters from the surface, in a temperature of about 20° C. The larvae grow rapidly during their first months, and in their first summer average about 25 mm. in length. They now move up into the uppermost water layers, the great majority being found between 50 and 25 meters or at times even at the surface itself. Then they commence their journey toward the shores of Europe, aided by the eastward movement of the surface water itself. During their first summer they are found in the western Atlantic (west of 50° long. W.). By their second summer they have attained an average length of 50–60 mm., and the bulk are now in the central Atlantic. By the third summer they have arrived off the coastal banks of Europe and are now full grown, averaging about 75 mm. in length, but still retaining the compressed, leaf-shaped larval form. In the course of the autumn and winter they undergo the retrograde metamorphosis which gives them their shape as eels and brings them to the elver stage, in which they move in to the shores and make their way up rivers and watercourses everywhere.

The average age of the elvers in spring is about 3 years. Many individuals, especially males, keep to the brackish water in lagoons or estuaries; others, especially females, move far up the streams they have entered and may in the course of their wanderings penetrate far into the interior of the Continent. In Switzerland, for instance, considerable quantities of eels occur, and specimens have been taken there in waters at an altitude of 3,000 feet above the level of the sea. The eels utilize their sojourn in fresh water to feed and grow big, but the duration of their stay here varies greatly, according to sex, climate, and quantity of food, ranging from about five to about twenty years or more. All the large eels are females; the males seldom exceed 45 cm. in length. During its period of growth the eel is of a yellowish or greenish color, with no metallic luster; these growing eels are generally termed "yellow eels." When they have reached the stage where the migratory instinct begins to assert itself the desire for food, otherwise voracious, is lessened, the body takes on a metallic sheen, and the pectorals become black and pointed. In this guise the eels are termed "silver eels," their flesh is very firm and rich in fat, and they are thus well equipped for entering upon their second and last great journey, this time back to the breeding grounds across the ocean."

Fig. 115 (p. 305) was made by Schmidt to show the distribution of the European eel and the American eel over the breeding grounds, the single lines denoting the former, the dotted lines the latter species. The heavily drawn innermost curve embraces the spawning areas; no leptocephali larger than 10 millimeters have been found within the ten millimeter curve, and so on, until the 45 millimeter curve, beyond which no larvae have been taken.

The hardest phase of the question to explain, and one which was insolvable to most imquirers, was the total absence of any European eel young along the American coast and of American eel young in European waters, in spite of the close proximity of the breeding grounds. Schmidt answers it thus: "In the case of the American eel, the pelagic larval stage is terminated in about one year; consequently the larvae have not time to make the journey to Europe, the distance being more than they can cover in that period. It is otherwise with the European eel, which takes nearly three times as long over its larval development, as a result of which practically all of them are far away from the western (American) portion of the Atlantic when the time comes for them, as elvers, to seek the coasts.

"We can thus indicate both a geographical and an ethological cause for the distribution of the two species of fesh-water eels. The former lies in the fact that *Anguilla rostrata* has its center of production somewhat farther west and south than *Anguilla vulgaris*. The latter is the different duration of the pelagic migratory stage. These two facts, in conjunction with the ocean currents as an aid to transport, and later—once the earliest stages of development are passed—the active movements of the larvae themselves, must be regarded as the causes which lead the two Atlantic species of eels to find each its own side of the ocean, despite the close proximity of their breeding grounds."

When we consider the fallacious beliefs regarding the various phases of the life history of the eel, which seem ludicrous in the light of this present knowledge but which were held with all good faith by foremost thinkers of their time, it is with hesitation that I dare associate the name of the American eel with the four eggs taken by the "Arcturus Expedition." As Ercolani in his essay "Del perfetto ermafroditismo delle Anguille" began: "the author this day appears before the academy with fear and trembling, since he intends to present something new regarding a question which has been the rock on which the vessels of so many distinguished scientists have foundered."

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